

Some habits of male horse-flies in Rhodesia (Diptera: Tabanidae)

by

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David Montagu Cookson, 1914-1966—A Tribute

David Montagu Cookson was born in London in March 1914, and educated at Harrow and Cambridge. After passing through the Officers Training Corps he served with the King's Own Scottish Borderers. During the Second World War he volunteered for the West African forces and was posted to the Gambia Regiment in which he served throughout the Burma Campaign. While holding the rank of Captain he was awarded the Military Cross for courage and leadership during persistent enemy attacks. He ultimately attained the rank of Major. After the war he settled on a farm in the Muden Valley of Natal with his father, Harold Cookson, to whom he was a constant companion for many years. Later they moved to the estate "Laurenceville" on the Vumba Mountains of Rhodesia. He participated with his father (a distinguished Lepidopterist) in collecting butterflies and hawk-moths, and made some notable discoveries in these groups. This collection soon was complete and he then became interested in obtaining specimens for the Natal Museum, and during the years 1962-1966 collected large numbers of Diptera in Rhodesia and Mocambique. In consequence of increasingly severe illness he underwent a major operation in St. Annes Hospital, Salisbury, where he died on 3rd August 1966.

It would be otiose to record that David Cookson was not a trained biologist: in fact, his powers of observation, meticulousness in everything he did, the excellence of his educational background, and his talent for lucid descriptive writing, enabled him to occupy himself with natural history matters in an unusually productive, useful and intelligent way. The perceptiveness he showed while assembling the data published below, the originality of his techniques, and the attention to detail—as well as the thousands of beautifully prepared specimens donated to the Natal Museum—are a testimonial to his excellence as a naturalist. The collection of Diptera he made is so extensive that it will require study over many years, but its value already is obvious as a number of new species have been described from it and many rare and remarkable forms have been noted for future attention.

At my request Mr. Cookson gave particular attention to collecting Tabanidae and proved adept at assembling long series of specimens in superb condition as well as finding uncommon species. A remarkable feature of his material is the high proportion of male horseflies; normally members of that sex are rarely caught because they do not suck blood and thus have no interest in humans or domestic stock, and frequently prefer habitats such as the forest canopy that are difficult to search. Mr. Cookson succeeded in catching the male of every species of tabanid living on the Vumba Mountains and made some interesting observations on their habits, so I suggested that he should prepare notes describing his collecting techniques and the biology of the males as far as possible. The article published below was received from him a few weeks before his death.

B. R. Stuckenberg

SYNOPSIS

Observations were made on sixteen species of Tabanidae in the Vumba Mountains of Eastern Rhodesia. Three distinct habits of the male tabanids were noticed, namely concentration around wet places, basking on stones or undergrowth, and swarming on hilltops. At wet places and in basking, females often accompanied the males but were seldom seen on hilltops. Species visiting wet places could be divided into those that settled on mud at the edge of water and those that dived at water (a habit largely confined to the males). Basking was observed to be a habit of only three species. Hilltop swarms were formed by males of two species of *Philoliteche*, one of which showed marked territorial behaviour.

INTRODUCTION

Information concerning the distribution and habits of African horse-flies has been mainly derived from adult females. Even the existence of a large proportion of species is at present known only by female specimens. This disparity in our knowledge of the two sexes is largely caused by the more noticeable feeding habit of the females. Though they are able

to feed on the nectar of flowers, the females alone are equipped with piercing mandibles that enable them to obtain the blood-meals from animals that are their primary source of nourishment. They can readily be found settling on animals or lurking in places frequented by them, and those diverted towards the collector quickly make their presence felt. The males, who lack these mandibles and are thus confined to a nectar diet, feed in a much less conspicuous manner. To illustrate how unobtrusive nectar-feeding is, inspection of a variety of Vumba flowers continued for a number of years resulted in the capture of a single female; yet the majority of both sexes, caught away from flowers, was dusted with pollen on mouth-parts and legs.

Most grateful thanks are offered to Mrs. P. J. Stuckenberg of Pietermaritzburg, Natal, who kindly provided a named collection of the Vumba horse-flies. The identity of all the species to be mentioned was established by comparison with specimens contained in this collection.

These notes are based on field observations made during several seasons on the northern slopes of the Vumba Mountains, eight miles south-east of Umtali. The district examined does not exceed three square miles in area, but within these limits it contains a considerable variety of vegetation, including montane forest, swamp, msasa (*Brachystegia*) savanna and open grassland, and ranges in altitude from 4,500 to 6,000 feet. The larger mammals, likely to be preyed on by female horse-flies, include bush-pig, baboon, Samango monkeys, some antelope and horses, besides a fair number of cattle.

Three distinct habits of male horse-flies were observed: (a) concentrating around wet places, (b) basking on stone or undergrowth, and (c) swarming on hilltops. At wet places and in basking the females accompanied the males, but they were seldom seen on hilltops.

CONCENTRATION AT WET PLACES

Most species of forest-dwelling horse-flies obtain moisture by settling on wet ground or by diving down at water. From late August, when horse-flies are first emerging, to early December, when the main rains begin, the Vumba is at its driest and surface water is confined to relatively few perennial swamps and streams. A further restriction is imposed by the strong partiality of the flies for a certain type of wet place: they prefer sunshine to shade, open spaces to those clogged with vegetation; for diving they prefer stagnant water to running water, and for settling they prefer fetid mud to clean sand. The most suitable places are usually to be found in swamps, where the sodden ground has thinned out both trees and undergrowth. To observe diving a large expanse of water is unnecessary; a puddle a few inches in diameter is sufficient.

Two good places, a quarter of a mile apart, were found in montane forest at a height of 4,500 feet. At the first, a disused irrigation ditch, passing through a glade, had become silted up with the best type of mud and was in sunshine throughout the day. At the second, a spring trickled into a pool a dozen square feet in area. Here the marginal mud was of poorer quality, and the overhead canopy did not permit the entire pool to be in sunshine. To begin with both places were left in their original state, the mud being covered with fallen leaves and branches, and churned up by cattle. Horse-flies that settled on this litter blended so well with their surroundings that they were frequently overlooked; when the net was placed over an observed fly there was virtual certainty that several unobserved ones would also be collected. So the rubbish was cleared away, the hoofmarks were smoothed out, and the mud was frequently splashed with water. These improvements greatly aided inspection.

Horse-flies of both sexes readily settled on mud, showing a preference for those parts that were in sunshine. The proportion of males to females varied with the species and also with the time of season; generally, in the early stages of emergence males were dominant, after a week or so females began to appear, and in the final period males were in a minority. For this reason it has not been possible to give reliable ratios for the sexes of any species. In their habits on the mud no difference was noticed between the sexes. They did not like walking. Those that chanced to alight on a dry spot slowly and laboriously crawled the inch or two necessary to bring them to moisture; if the distance was much more than that, they covered it by taking flight. Those that alighted on a moist spot remained sedentary, not using their legs except to make a slight shuffle immediately after settling, as though easing themselves into a comfortable position. The length of stay on the mud was usually between one to two minutes for most species, and this time tended to become shorter as the day advanced. Body movements were mainly confined to prodding the mouth-parts into the mud and to twitching of the rear abdominal segments, but occasionally a fly would use the mud as a base for toilet operations, grooming its head and wings with its forelegs, and would fly away without sipping. Unlike butterflies, no horse-fly was seen to discharge fluid from the anus while on the mud. When engaged in sipping, horse-flies ignored other horse-flies and other insects: no instances of aggression or copulation were observed.

Settling on the mud was a habit shared by both sexes of all the observed species, whereas diving at the water was a specialised habit displayed by three species and largely confined to males.

Species seen to dive at water

Cydistomyia (Amanella) imbecilla (Karsch). This was the earliest species to emerge, appearing in late August; by the end of September it was abundant, and continued to fly in diminishing numbers until the middle of November.

The habit of diving was strongly developed in the males, and to a lesser extent in the females, of this species, and whether they chose to dive or to settle depended mainly on the distribution of light and shade. If sunshine fell mostly on the pool, diving increased; if it fell mostly on the margin, settling increased; and if pool and margin were both in sunshine, the number diving approximately equalled the number settling. The mode of diving varied in details. Generally, the flies were first sighted approaching the pool in fast level flight, and from six to twelve inches above the surface. When they were over the water, they sometimes showed hesitation by making a check in speed, a sharp turn, or an undulatory motion, before plunging downwards at an almost vertical angle. Often no hesitation was displayed, and the flies descended immediately at a less steep angle and on direct or spiral courses. The force of contact with the water ranged from an inconsiderable graze to an impact sufficient to cause a splash and a series of ripples. The speed of the action was too rapid to permit observation of what occurred at the moment of contact; it is probable that beads of moisture were picked up on the mouth-parts and legs, and these were carried away and absorbed at leisure. The flight on leaving the water was always rapid and decided, and the flies showed an inclination for making a complete about-turn; those that dived steeply departed steeply, and those that dived at an oblique angle departed at a similar angle and in the direction of their arrival. The departing flies



Fig. 1. *Cydistomyia (Amanella) imbecilla* (Karsch) ♂ on mud.

either continued until they were out of sight, or else quickly turned aside to settle on the mud or the dry leaves of the forest-floor.

Less often the dive was multiple; after the first dive, in which contact with the water was made in the normal fashion, the flies climbed a few inches and then returned to the water for a second and, rarely, a third dive before departure. Other variations, infrequently seen, included: dives at the mud, dives that failed to reach the water, and dives in which the flies remained a second or two motionless on the surface.

Since there was no means of determining the sex of a flying individual of this species, efforts were made to collect flies as they departed from a dive. Owing to their speed the percentage of success was not high, and most were caught in the earlier part of the morning when the flies were sluggish. In September, out of about sixty specimens all but two were males; in October, out of about forty all but eight were males.

The species also settled readily on mud, where, by October, females were as plentiful as males. Both sexes were fond of settling on floating leaves to sip over the side, as well as settling directly on the water to sip from the surface.

At the height of its season, an average of two corpses of the species, either male or female, were found floating in the pool every day. No corpses of other horse-fly species were observed. Diving seemed the most likely cause of these fatalities, but none of the many thousands of dives witnessed ever ended in misadventure. Excluding minor mishaps, such as landing upside down on the mud, four serious accidents were seen: one male, on leaving the mud, flew straight into the pool, and one male and two females, sipping at mud close to the margin, slipped off and got their wings into the water. In each instance the fly was unable to climb ashore on account of surface tension. As the great majority of the corpses were already in the water when the day's observations began, it seems probable that early arrivals, settling near or on the water whilst semi-torpid, were the chief victims.

Chrysops laniger Loew. Moderate numbers of this species visited the pool or the ditch to dive at the water during the midday heat of October. Its habit of diving was most pronounced: in fact only two individuals of the species have been seen to settle; a male that alighted on the mud and a female that perched on a fern overhanging the pool.

All the dives witnessed were multiple. On arrival the flies skimmed over the water in a darting flight from one to six inches above the surface, and avoided flying over the margin by making continual sharp turns. Though the speed of flight remained constant, the rapid changes of direction conveyed an impression of extreme jerkiness. After five or more seconds of flight, the flies dived down and brushed the surface so delicately that no ripple was raised, and then they resumed their darting flight for a rather shorter time before carrying out another dive. On an average they made three dives in the course of a single visit, and nearly always departed promptly after the final dive, although a brief valedictory flight was sometimes observed. Contact with the water was usually made without check in flight, but on one occasion a definite glimpse, lasting about half a second, was obtained of a male stationary on the surface in the first dive of a series. Both sexes behaved in the same fashion, though females were seldom seen.

Chrysops magnifica Austen. The habits of this species were similar, but not identical, to those of *C. laniger*. Both species shared the darting flight before diving, but whereas *C. laniger* was equally active above pools or puddles, *C. magnifica* regulated its speed to the area of water. At the pool it flew as fast as *C. laniger*; at a puddle its flight was slow and deliberate. It usually departed after a single dive, though sometimes lingering to make a second. It was also far more inclined to settle, either on the mud or on the surface of the water. Both in diving and in settling males outnumbered females.

A pair of this species, settled in copula on the underside of a leaf, was caught in the forest a hundred yards from the pool.

Species not seen to dive at water

Haematopota nobilis (Grünberg). A common species. On arrival the flies usually flew rapidly over the mud, making two or three circuits, as though undecided where to settle. Once a place had been chosen, they remained motionless for longer than any other species; five minutes was a normal time, and on occasion this was protracted to ten minutes. Settling on the mud was largely a male habit, though females were present in the area to such an extent that their buzzing and biting were disagreeable distractions. One female was seen to fly very slowly, almost to hover, over the surface of the pool and to dab herself several times against the water. This behaviour was not repeated, and must be considered an individual eccentricity.

Haematopota nigripennis Austen. The main brood of this species emerges in autumn, when the forest is uniformly soaked by the rains and the need for horse-flies to concentrate around particular wet places has passed. A few males were caught on mud in various parts of the forest.

Haematopota ingluviosa Austen. Another common species, emerging in early spring. Though both sexes settled plentifully on the mud, they were not seen in the drier parts of the forest.

Haematopota divisapex Austen. Judged by the number of females seen, this species ranked

as by far the commonest horse-fly on the Vumba. The females were attracted by movement and settled in abundance on the skin and clothing of any person walking through the forest, but if the person kept still they rapidly lost interest and flew away without biting. At the mud females were also seen in large numbers, arriving silently and unobtrusively to merge into the brown background. It is reasonable to suppose that an equivalent number of males exist in the forest, but their principal habitat has not been discovered. A few males settled on the mud, where their large pale eyes rendered them much more obvious than the camouflaged females.

Tabanus insignis Loew. A moderately common species, most plentiful in December. Both sexes, in approximately equal numbers, came to the mud, arriving at high speed and settling without hesitation. In the first moment after alighting, before they had begun to sip, they were alert and watchful, and the most furtive movement of the net was sufficient to alarm them.

Tabanocella denticornis (Weid.). One male settled on a reed in a bog.

Tabanus atrimanus Loew. A less common species than *T. insignis* and with similar habits. The males were slightly outnumbered by females.

Euanca maculatissima (Macquart). The arrival at the mud of this large and gaudy species was heralded by the low-pitched drone of its flight. Usually it settled without hesitation, but sometimes it circled once or twice and departed without settling. It seldom remained for longer than a minute, and during this time it sucked voraciously—sipped is too genteel a word to describe its behaviour—with the head prodded downwards and the abdomen pulsating rapidly backwards and forwards. Of the score of specimens seen one only was a male.

BASKING

Philoliche (Philoliche) aethiopica (Thünberg). In montane forest this was quite a common species. It avoided the thicker parts of the forest and showed a strong preference for glades and open places, where both sexes chose sunny perches a few feet from the ground on rushes, grasses, and shrubs. In habits it was languid; specimens could easily be coaxed to leave their perch and crawl on to a finger. When it did take flight, it immediately resettled a few yards distant on a similar perch. It was not seen to visit the mud.

Cydistomyia (Amanella) cooksoni Usher. This species, discovered on the Vumba, was for several seasons considered to be rare. Males came to the mud sporadically, and females were hardly ever seen. However, it was later found that the species had a strong habit of basking on the verandah of a house, some fifty yards from the edge of montane forest. If there were no clouds, the flies arrived between two and three hours after sunrise, and were not seen thereafter; if the day was overcast, the flies arrived at any time. Both sexes had this basking habit, but the first females did not appear until a month after the first males.

Tabanus taeniola de Beauvois. A single male was caught on the same verandah during December.

SWARMING ON HILLTOPS

Swarms of male horse-flies were observed on several Vumba hilltops, at altitudes varying from under 5,000 feet to over 6,000 feet. All the hills were within an area of three square miles, all were covered by a comparable type of vegetation, and all had a similar



Fig. 2. *Philoliche (P.) aethiopica* (Thünberg) ♂ basking.

type of rounded grassy summit. On one particular hilltop a swarm of a dozen or more males was frequently seen, whereas on the other hilltops a swarm of more than three males was quite noteworthy. The prolific hill was the only one to be grazed by cattle, which were seen to be molested by numbers of female horse-flies, and it thus seems likely that the large swarm of males on the summit was related to the supply of accessible females on the lower slopes. From their size the females almost certainly belonged to the genus *Philoliche*, but the cattle, no doubt through being bitten, were highly restive and all attempts to secure specimens, or to obtain visual identification, were failures.

This particular hilltop reached a surveyed height of 5,990 feet and consisted of a two-acre plateau, where a waist-high growth of bracken and woody plants was separated into clumps by corridors of grass. At its west side the plateau sloped down into a small depression sheltered from the prevailing easterly winds. Swarms were seen here on all sunny days during the season. Each species tended to have its favourite swarming-site on the hilltop, for the most part on the west side of the plateau, and the exact position of the swarm varied slightly from day to day, according to the strength and direction of the wind. *Philoliche (Phara) rubramarginata* (Macquart). This species emerged early in September and was not particularly common. The swarm seldom exceeded six males, and by the end of September only single individuals were to be seen. The male was inactive and showed a fondness for perching on the top of low-growing plants, not more than two feet from the ground; whilst so perched he was not shy and allowed himself to be touched before flying away. In an occasional outburst of restlessness a male might change position five or six times within the minute, trying different footings on the same plant or on another plant

close by. Once a satisfactory perch had been found, he would remain immobile for ten minutes or more. Flights, when they were made, covered short distances at leisurely speed, and hugged the ground along openings in the vegetation. Hovering was not observed. Towards each other, males behaved in a placid and easy-going manner; at intervals one would chase another in a perfunctory fashion for a few yards, and then pursuer and pursued would return to the starting point and settle on adjacent perches.

Philoliche (Phara) speciosa bracteata (Austen). This and *bicingulata*, next to be mentioned, appear to provide an instance of sympatric subspecies. It flew from the middle of September until the end of October, and at its peak period formed a swarm of about two dozen males. In sunshine the swarm was continually air-borne, but whenever the sun moved behind cloud the males settled. The position of the swarm covered an area of fifty yards along the west edge of the plateau and ten yards in width; in a strong easterly wind it moved a short distance into the shelter of the western depression.

In the early or late part of the season, when the number constituting the swarm was small, the males spaced themselves out and each occupied a sizable territory of his own. In this territory the male hovered, head into the wind, about three to four feet from the ground and flush with the top of the highest vegetation. The hovering was not stationary; there was a sideways drift, as well as a fluctuation in height. After a few minutes, hovering was replaced by a sweeping curved flight, covering ten or more yards and rising twelve feet from the ground. When this had been carried out, hovering was resumed, but in a position some yards from the original site. After four or five repetitions of these flights, the male might have moved his hovering position by twenty yards. When the number in the swarm was large, the individual habit was modified by shortage of space; the territories of each male were smaller, and the sweeping flights and the changes in hovering position were no longer observed.

The males were aggressive, and readily relinquished their hovering in order to pursue other flying insects that intruded into their territories. This harrying was confined to intruders at, or above, the hovering level of the males; any trespassers in the space beneath them were disregarded. Males, watched on different occasions, were seen to repel a succession of wasps, dragonflies, beetles, butterflies (mainly of the genus *Charaxes*), and large bombyliid flies of the genus *Exoprosopa*; yet they were seemingly blind to numbers of *P. rubramarginata* that were flying and settling a couple of feet below them. However, the principal quarry was another male of the same species. The hovering drift was continually bringing two neighbours sufficiently close for one to become aware of the other, and at once the quiet drone changed to a sharp buzz, and the couple would vanish swiftly from sight. The pursuit was not protracted, and the two territories were soon reoccupied, presumably by the same two males.

Philoliche (Phara) speciosa bicingulata Oldroyd. A subspecies that flew from early October until late December, and thus overlapped with *P. bracteata*. The males were more numerous than those of *bracteata*, and their individual habits were identical. However, the *bicingulata* swarm occupied an area around the periphery of a clump of trees in the depression to the west of the plateau, and about fifty yards distant from the *bracteata* swarm. This slight difference in position was noticed from day to day, and from season to season.

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